Distribution and Stability of Grasslands in the Los Angeles Basin

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Abstract. - Present grassland distribution (as of 1980) was mapped from modern aerial photographs for 21 7.5 minute quadrangles in the Los Angeles Basin. These patterns were compared with the distribution of grasslands mapped from aerial photographs from 1928 to 1936. Grasslands increased in all but three quadrangles, the greatest increases being in the northwestern portion of the basin. Vegetational changes, however, were not unindirectional as shrubland, notably coastal sage scrub, replaced grassland in sections of nine quadrangles. In general, areas subject to frequent fires and grazing moved from shrubland to grassland while grassland areas with infrequent disturbance were invaded by shrubs. An intensive study was undertaken in a quadrangle in which vegetation had changed in both directions. Nine islands of coastal sage scrub surrounded by grassland were selected for study. Vegetation pattern was not dictated by topographic position or soil charateristics. Density of seedlings was high within patches of mature shrubs but seedlings were largely absent outside their boundaries. Shrub sizes in transects across the ecotone suggested that in eight of the nine coastal sage scrub patches shrubland was not invading grassland. Recent burning (within 10 years), coupled with intensive grazing, appears to inhibit the invasion of shrubs into adjacent grasslands. We hypothesize that the vegetation of the Los Angeles Basin is a mosaic of community types differing in their tolerances to disturbance.

Annual grasslands are a major vegetation type in California. Throughout much of their range they are dominated by non-native species and the vegetation composition prior to the introduction of these exotic species in the late 18th century is unknown. One hypothesis is that these grasslands were originally dominated by native bunchgrass species, notably *Stipa pulchra*. An alternative is that these regions were originally brush covered.

Clements (1934) noted that certain grassland areas contained isolated patches of *Stipa pulchra* which he interpreted as "relicts" of a previous native grassland. It has been suggested that these native grasslands succumbed to competition with annual exotics during periods of intensive grazing and drought in the mid 19th century (Heady 1977). Alternatively, Cooper (1927) noted what he interpreted as "relict" stands of brush in grassland areas and hypothesized that early settlers cleared brushlands by repeated fires. Since brush species are intolerant of repeated fires they were replaced by the exotic annual species which are good colonizers.

Wells (1962) suggested that the present annual grasslands were not derived from grasslands dominated by native perennial bunchgrasses on deep clay soils, but were derived from woody sage and chaparral vegetation on shallow rocky soils.

Today, areas dominated by native grasses are invariably on fine-textured substrates. Attempts to regenerate native grass species off such soils have largely failed (Kay et al. 1981). Although the theory of widespread native grasslands is based largely on "presumed relicts" of *Stipa pulchra* and other native grasses, the alternative theory is based on "known relicts" of chaparral. Documents show that many grassland areas once were covered by brush. Land managers have long used repeated prescribed fires to clear brush and Zedler et al. (1983) have shown this can result from frequent wildfires.

Annual grasslands are widely distributed throughout the Los Angeles Basin. The purpose of this study was to determine the distribution and stability of these grasslands and to identify the factors responsible for their formation. A major focus was to document present grassland distribution and determine if any distributional changes had occurred in the last 50 years by comparisons with early aerial photographs. A second focus was to examine site characteristics in a grassland area containing patches of coastal sage scrub. Demographic trends of shrubs at the grass: sage interface were examined in order to evaluate the stability of such zonation patterns.

Sites and Methods

Present and Past Grassland Distribution

Twenty-one 7.5-minute USGS quadrangles were selected for study. These included the most extensive grasslands in the Los Angeles Basin (Fig. 1) excluding the Santa Monica Mtns. where grassland distribution has been studied by Goode (1981) and Hobbs (1983). USGS quadrangle maps were used as a starting point for outlining the present-day grassland distribution. These maps give vegetation types, although in many cases they are out of date. Therefore, 1974-1976 aerial photographs were obtained for all quadrangles and used to update vegetation distribution. Updated maps were further checked by on-site inspection of most areas in 1979-1980. The historical record for these areas was constructed by examination of 1928-1936 aerial photographs from the Fairchild Collection at Whittier College, Whittier, California. Interpretation of these photographs was aided by vegetation maps produced by Wieslander circa 1930 (available at the Rancho Santa Ana Botanic Garden). USGS topographic maps were also a source of historical data since vegetation types were mapped, but often not updated for over 25 years. All historical vegetation data were mapped on acetate sheet overlays of the 7.5-minute topographic maps. From the present-day vegetation maps and historical overlays, the total area of vegetation change was estimated to the nearest hectare.

Data on the fire history were gathered from county, state, and federal agencies for areas where such data were available. For various reasons the area under study has very incomplete data on fire history. USDA soil survey maps were consulted for areas for which they were available.

Localized Patterns at the Grass: Sage Ecotone-Intensive Site

The intensive study site was the Calabasas Quadrangle between Palo Comado and Cheeseboro Canyons, 3-5 km N of Hwy 101. This area contains a mosaic of grasslands with patches of coastal sage scrub. Nine sites were selected; each included one scrub patch plus adjoining grassland.

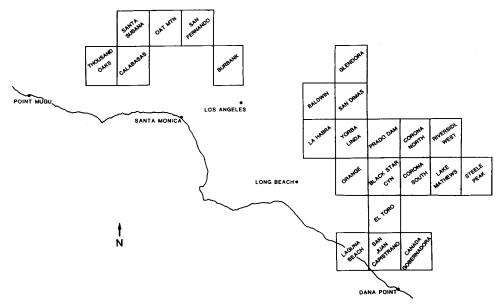


Fig. 1. Los Angeles Basin 7.5 minute quadrangles included in this study.

Slope aspect and inclination were recorded for each site. Soil samples from 0-15 cm depth were taken from the shrub stand and adjoining grassland, in most cases on two sides. For each soil sample, pH, organic matter content and soil texture were determined according to procedures in Cox (1980).

Vegetation at each site was sampled in spring 1982 by recording height and foliage diameter of all shrub species in 3.5×4.0 m quadrats placed contiguously from grassland through the coastal sage scrub patch and into the grassland on the other side.

Results

Grassland Distribution

During the past 50 years, vegetation has changed throughout the Los Angeles Basin (Table 1). Since urbanized areas and other human artifacts such as agricultural land have been excluded from this analysis, decreases in one vegetation represent an increase in another vegetation type. Grasslands have increased or decreased in many areas. Quantitatively, the major change has been an increase in grasslands at the expense of coastal sage scrub and chaparral. A brief description of the changes observed in each quadrangle follows.

Northwestern Los Angeles Basin

In the Thousand Oaks Quadrangle, coastal sage increased extensively at the expense of grassland over the past 40 years. This is evident in a comparison of 1936 aerial photos with the 1952 USGS topographic map. Further increases in coastal sage scrub were seen in the 1976 aerial photo. Except for a small fire around Medea Creek in 1970, this region had not burned since 1910. The area burned in 1970 was grassland in 1976. In general, grasslands predominated on

	Area changed	Area subject to change		Grasslands	
Quadrangle	(ha)	(ha)	% change	Increase	Decrease
Northwestern:	*************************************				
Thousand Oaks	400	8000	5	X	X
Calabasas	700	12,000	6	X	X
Santa Susana	1000	12,000	8	X	
Oat Mountain	300	12,000	3	X	
San Fernando	1100	8000	14	x	
Burbank	50	8000	>1	X	
Northeastern:					
Glendora	400	15,000	3		X
San Dimas	500	8000	6	X	X
Baldwin Park	0	1700	0		
La Habra	300	4000	8	X	
Yorba Linda	200	23,000	2	\mathbf{x}	
Prado Dam	250	10,000	2		X
Corona North	20	1500	>1	X	
Riverside West	100	1500	6	X	
Southern:					
Steele Peak	600	8000	8	X	X
Lake Mathews	1500	12,000	13	\mathbf{x}	X
Corona South	100	12,000	>1	X	
Black Star Canyon	100	12,000	3		X
Orange					
El Toro	150	8000	7	X	
Canada Gobernadora	500	16,000	2	X	X
San Juan Capistrano	100	16,000	>1	X	
Laguna Beach	900	9000	10		X

Table 1. Grassland distribution changes in the Los Angeles Basin between 1928 and 1980.

soil such as Linne silty clay (30–50% slope), Rincon silty clay loam (2–9% slope) and Cropley clay (2–9% slope). Coastal sage tended to predominate on Calleguas shaley loam (30–50% slope). However, field examination detected numerous exceptions.

In the Calabasas Quadrangle, grassland has increased substantially, particularly in Las Virgenes, Cheeseboro, and Palo Comado Canyons. Increases were evident from 1928 to 1952, and from 1952 to 1976. Most of this area burned in 1970 and is now grazed by cattle. A small area in the southern portion showed an increase in coastal sage scrub over grassland, however.

The Santa Susana Quadrangle was dominated by grasslands in 1930. Since then, these grasslands have expanded at the expense of coastal sage scrub along Chivo, Gillibrand, Windmill, and Meier Canyons. The last known fire in this area was in 1970, 10 years prior to these observations. Today this area is heavily grazed by cattle. An area within a fenced-in water tank remained coastal sage while grassland replaced coastal sage outside. A 1-ha area of grassland, which appeared to be under cultivation in 1928, was coastal sage scrub in 1980.

Grasslands increased substantially on the south-facing slopes of the Santa Susana Mountains in the Oat Mountain Quadrangle. However, a few patches of

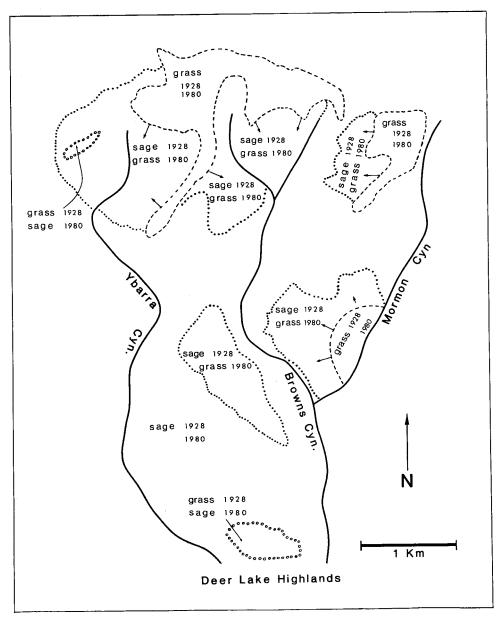


Fig. 2. Historical and present day vegetation patterns (as of 1980) on a portion of the Oat Mountain Quadrangle.

coastal sage scrub appeared in 1980 in areas that were grassland in 1928. These changes are illustrated in Fig. 2. Parts of this area burned in either 1969 and/or 1970. Most of this area is currently grazed by cattle.

In the San Fernando Quadrangle, grassland has increased markedly since a fire in 1975. Shrub resprouts were most evident on north-facing slopes and ravines, however, and the entire area is likely to return to the dense chaparral recorded on the 1966 USGS map.

The vegetation of the Verdugo Mountains within the Burbank Quadrangle has remained unchanged, although the density of chaparral between Elmwood and Stough Canyons has increased since 1928.

Northeastern Los Angeles Basin

Glendora Quadrangle includes the USDA San Dimas Experimental Forest. A large section of chaparral in this area was converted to grassland as part of a type-conversion experiment.

Within the San Dimas Quadrangle there have been diverse changes. Three hectares on the south facing slope of Buzzard Peak were coastal sage or chaparral in the 1928 aerial photo and Wieslander's 1930 vegetation map. On the 1964 USGS map they were sparse shrub-grassland and in the 1975 aerial photo and 1980 field checks they had progressed to pure grassland at the lower elevations and open grass-shrubland higher on the slope. Several areas in this quadrangle had changed from grassland or sparse shrub cover circa 1930 to dense brush in 1980; e.g., east of Diamond Bar, within the Puddingstone Reservoir State Recreation Area and northeast of Tonner Canyon.

The Baldwin Park Quadrangle has remained relatively stable. Wieslander mapped this area in 1930 and much of his grassland-coastal sage scrub mosaic was still evident in the 1976 aerial photo. Much of this area burned in 1976.

In La Habra Quadrangle grassland increased somewhat at the expense of coastal sage scrub or chaparral, especially in the proximity of oil fields which were not present in 1928.

Parts of the Puente and Chino Hills, included in the Yorba Linda Quadrangle, have remained quite stable over the past 50 years despite the considerable mosaic of vegetation. Aerial photos showed that from 1928 to 1975 the density of scrub oak chaparral increased between Soquoel and Telegraph Canyons. An area along Brea Canyon Road burned in 1970, and the 1975 photo showed no change in vegetation since 1928 other than more open chaparral due to incomplete recovery from the fire. Soil maps for the San Bernardino section of this quadrangle showed that both grasslands and shrublands occurred on Fontana clay loam and Gaviota rock outcrop complex soils.

The vegetation in the Prado Dam Quadrangle has remained relatively stable over the past 50 years. One obvious change is a decrease in live oak (Quercus agrifolia) density in this region. The soils of the San Bernardino County portion of this quadrangle have been mapped and no obvious correlation exists between soil type and vegetation; scrub, grasses, and oak trees were found on Alo clay and Fontana clay loam as well as on the Gaviota rock outcrop complex. Topography seemed to be important since coastal sage scrub was concentrated on steep slopes, grassland on valley floors, oak woodland on gentle slopes and stream floodplains.

The Corona North Quadrangle was dense coastal sage scrub in 1931; however, the 1967 USGS map indicated it was <25% shrub cover and in 1980 it was still sparse coastal sage scrub. This may derive from a fire which covered most of the area in 1959.

Three hectares on the north facing slope of Arlington Peak in Riverside West Quadrangle were dense coastal sage scrub in the 1975 photos but burned in 1978. Field observations in 1980 indicated that these areas were predominantly grass covered.

In 1931, the Pedley Hills were covered by coastal sage which was denser on north-facing than on south-facing slopes. This area burned in 1970 and in 1975 was covered by a mixture of grass and sage.

Southern Los Angeles Basin

Steele Peak Quadrangle has had several changes in the valleys. An area adjacent to the Galvian Mine was partially cultivated and entirely grassland in 1930; however, the eastern three quarters of the valley was sage in 1980. Many of the other valleys covered by grassland in 1930 are now orchards and not considered in the estimates in Table 1. Several areas of rugged terrain southwest of Steele Peak were covered with sage in 1931 but were dominated by grassland in 1980. In general this replacement of coastal sage scrub by grassland did not occur on north-facing slopes. Between 1960 and 1979 there were at least five fires in various parts of this region.

In the Lake Mathews Quadrangle large areas that were grassland in 1930 are now coastal sage scrub. This area was heavily grazed in the 1930's and before. In the 1950's, as part of the Lake Mathews Reservoir project, a chain-link fence was constructed around much of the area. This fence bounds the area which has gone from grass to shrubland, possibly due to the elimination of grazing plus the fact that there have been no recorded fires since 1910. A small area outside this fence site, which was dense coastal sage scrub in 1974, burned in 1978. In 1980 it was still dominated by grasses and a few resprouting shrubs. Another site was dense coastal sage in 1930, burned in 1957, and was still sage in 1974.

The Corona South Quadrangle showed some expansion of grassland at the expense of coastal sage scrub.

In the Black Star Canyon Quadrangle some area has gone from woodland to grass and several hectares of grassland have been invaded by coastal sage scrub. In the northern half of the quadrangle the chaparral vegetation has become noticeably sparser since 1931. This area burned in 1948 and 1967. The chaparral east of Black Star Canyon has not burned since 1914 and is considerably denser than in 1931. A grassland area north of Fresno Canyon to the Santa Ana River burned in 1928, 1958, and 1967 and was still grassland in 1975.

The Orange Quadrangle was largely grassland in 1928 and remains so today. Riparian woodland has declined in the Peralta Hills and sage scrub is less extensive along the lower hills around Chapman Ave.

The hills above Rattlesnake and Siphon Reservoirs in the El Toro Quadrangle were sage in the 1931 photo and grassland in the 1974 photo. These areas burned in 1948 and 1967. The coastal sage on the hills between Williams and Silverado Canyons was denser in 1974 than in 1931.

Within the Canada Gobernadora Quadrangle pockets of coastal sage surrounded by grassland were evident in 1929. By 1974 the coastal sage had expanded and dominated the area, particularly the region west of Trampas Canyon. The scrub cover was also denser in 1929 than in 1974. A similar pattern was evident along the eastern wall of Bell Canyon. In 1958 wildfire burned from Canada Chaquita east into the Cleveland National Forest. An area near Trampas Canyon that escaped this fire showed an increase in density of scrub.

Much of the open area within the San Juan Capistrano Quadrangle has remained grassland over the past 50 years. This area has been cultivated and grazed heavily.

A 1-ha patch on the western bank of Arroyo Trabuco was coastal sage in 1929 and grassland in 1974.

In the Laguna Beach Quadrangle many localities changed from grassland in 1931 to sparse coastal sage scrub in 1964, and to dense coastal sage scrub in 1980: e.g., Emerald, Laguna, East Moro and Los Trancos Canyons, and the southwest-facing slopes of Mustard Hill. The 1964 USGS indicated that the San Joaquin Hills had <25% coastal sage coverage, whereas the 1974 photos and 1980 field checks showed this area to be dense coastal sage scrub. Today most grasslands are on 9–50% slopes on Alo clay or Balcom clay loam. Much of the coastal sage is on 30–75% slopes on Cieneba rock outcrop complex and Callegaus clay loam. However, there were numerous exceptions. These areas have not burned since 1931. This quadrangle was heavily grazed by sheep in the late 1800's and early 1900's (Fusch 1968) but is no longer being grazed.

Localized Patterns at the Intensive Study Site

The study area was in the Calabasas Quadrangle and had not burned for 10 years as indicated by ring counts of *Salvia leucophylla* shrubs. This corresponds to the Clampitt Fire of 1970. This area has been intensively grazed in recent years.

The nine patches of coastal sage scrub were distributed on a range of slope aspects and inclinations (Table 2). Observations of these and other sage patches confirmed that they are not related to topographic position. Soils data likewise suggest that they are not distributed according to soil differences. Grassland soils tended to be more similar to those of adjacent sage stands than to those of other grassland areas (Table 2).

A reasonable hypothesis is that the mosaic of coastal sage patches in grassland is a dynamic system controlled by disturbance. If the boundaries between these communities are changing, then in what direction? Is coastal sage invading grassland or vice versa? Leak and Graber (1974) suggested a technique for determining the direction in which a shrubland-grassland boundary is moving. Their theory suggests that if sage scrub species are advancing into grassland, one should find an advancing front of young plants. On the other hand if the grasslands are gradually replacing the sage, perhaps due to disturbance such as frequent fires, the sage plants along the margins should be as old as those throughout the stand. A rough test of this prediction was made by examining the distribution of shrub heights, as height and age are related in these shrub species.

Figure 3 shows such a height profile for a belt transect 4 m wide through Site 1. In this stand Salvia leucophylla was the dominant shrub (Table 3). It is clear that the distribution of size classes is not greatly different in the border areas as compared to within the stand itself; mature shrubs occurred in the ecotone as well as within the stand. Seedlings (plants <25 cm high) were abundant (Table 3) within the stand but not at the advancing front. Seven of the other eight sites showed a pattern broadly similar to Site 1.

Site 2 was co-dominated by Salvia leucophylla and Artemisia californica (Table 3). One difference from the Site 1 pattern was that while seedlings were not found outside the boundary of the stand, there was an area within the stand devoid of mature shrubs (possibly from disturbance) but with abundant seedlings and "saplings." This area extended for three quadrats (out of 22) and had 1.9 seedlings/ m^2 compared to $<0.1/m^2$ in all other plots.

Table 2. Slope aspect and inclination for each coastal sage patch studied and soil characteristics within each stand and in the adjacent grassland in the Calabasas Quadrangle.

Site Area		Inclina-		Soil characteristics					
			pН	Organic matter (% dry weight)	Texture (%)				
	Aspect	(°)			Clay	Silt	Sand	Gravel	
#1	Upper grass	N	20	6.5	6.7	15	11	74	1.1
	Shrubs			7.5	8.9	10	14	76	7.1
	Lower grass			7.8	7.9	6	17	77	6.1
#2	Upper grass	WNW	30	6.5	7.3	11	11	78	0.2
	Shrubs			6.7	6.2	9	12	79	0.5
	Lower grass			7.6	8.8	11	12	76	3.4
#3	Upper grass	NNW	35	6.8	7.5	11	13	76	2.0
	Shrubs			6.9	7.9	10	13	77	2.9
	Lower grass			6.7	7.0	10	12	78	3.7
#4	Upper grass	NW	25	6.9	8.2	9	14	77	4.2
	Salvia			6.7	11.8	12	13	75	9.0
	Haplopappus			6.8	8.0	12	12	76	5.5
	Haplopappus		15	6.5	7.5	14	10	76	2.6
	Lower grass			6.4	7.0	13	13	74	6.5
#5	Upper grass	E	25	7.7	6.0	7	16	77	0.4
	Shrubs			7.2	6.2	9	11	80	1.5
#6	Upper grass	NW	40	6.7	6.9	11	10	79	0.1
	Shrubs			6.7	6.8	9	11	80	0.9
	Lower grass			6.9	6.9	8	13	79	3.6
#7	Upper grass	\mathbf{w}	30	7.6	8.4	9	15	76	6.2
	Shrubs	,		7.5	9.1	8	14	78	5.0
#8	North grass	ESE	15	7.8	5.6	8	12	80	1.7
	Shrubs			7.8	6.3	7	15	78	3.2
	South grass			7.7	6.4	7	13	80	2.6
#9	Upper grass	N	30	6.5	6.8	11	11	78	1.0
	Shrubs			6.8	6.6	10	11	79	1.1
	Lower grass			6.6	6.4	8	13	79	7.5

Salvia leucophylla and Artemisia californica dominated Site 3. One variation from the pattern seen for Site 1 (Fig. 3) was that half of the site lacked seedlings altogether whereas the other half had a seedling density of 0.6/m².

Figure 4 shows the profile observed in Site 4 which showed the greatest deviation from the pattern noted at Site 1 (cf. Fig. 3). The area was dominated by *Haplopappus venetus*. The distribution was the closest example we observed of a shrub population expanding outward into the grassland.

Salvia leucophylla dominated Site 5 and all shrub seedlings were within the boundary of the largest shrubs.

Co-dominants at Site 6 were Salvia leucophylla and Artemisia californica. This stand had an abundance of seedlings which followed a pattern comparable to Fig. 3 although the greatest concentration of seedlings was in the center of the stand.

Site 7 was essentially pure Salvia leucophylla and no shrub <50 cm height occurred within 12 m of the outer boundary of the stand.

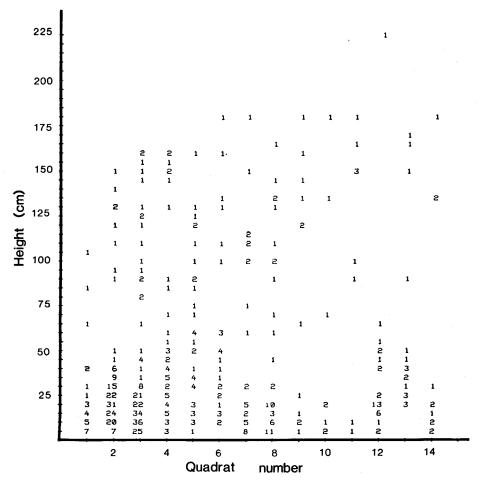


Fig. 3. Shrub height profile for 4 m wide 3.5 m deep contiguous quadrats through Site 1 in the Calabasas Quadrangle (number of individuals in 5 cm size class are plotted). Sampling began and ended in pure grassland although for presentation only the first and last quadrats with shrub species present are included.

Shrub height distribution at Sites 8 and 9 followed closely the pattern observed at Site 1 (Fig. 3).

Discussion

We believe that Well's (1962) model of grassland dynamics applies well to the Los Angeles Basin. He argued that the vegetation patterns in the coastal ranges of California are determined largely by different tolerances to disturbance and by different colonizing abilities. Grasslands represent the rapid-recovery extreme of a continuum of resilience. This community persists under intensive grazing and frequent fires. Coastal sage scrub, due to its subligneous character, falls between grassland and chaparral with respect to its resilience to disturbance. Coastal sage recovers rapidly after fire from resprouts, although seedling establishment is poor in the first post-fire season (Keeley and Keeley 1984). Fires in successive or

		Relative density (%)								
Species S	Site:	1	2	3	4	5	6	7	8	9
Salvia leucophylla		92	60	85	26	85	82	99	79	5
Artemisia californica		1	35	14	3	2	18	1	6	67
Haplopappus venetus		5	4	1	71				15	28
Malacothamnus fasciculatun	ı		1			13				
Eriogonum fasciculatum		2								
Shrub seedlings/m ²		2.1	0.3	0.3	13.5	< 0.1	5.9	0.2	<0.1	2.9

Table 3. Shrub density in nine coastal sage sites in the Calabasas Quadrangle.

alternate years are highly destructive to coastal sage scrub species (Zedler et al. 1983). Chaparral regenerates after fire with resprouts and seedlings but requires the longest fire-free period to maintain itself (Keeley 1981).

The Los Angeles Basin in prehistorical times was likely dominated to a great extent by ligneous formations such as chaparral and oak or walnut woodlands. Natural lightning fires were a source of wildfires although there is reason to believe the frequency of such disturbance was lower than at present (Keeley 1982). Even then, boundaries between communities were probably dynamic, due to the random nature of wildfires or disturbances from the large grazing fauna (Stock 1956). Grasslands at that time may have been dominated by *Stipa pulchra*, particularly on heavier clay soils, although annuals were undoubtedly important components (Wester 1981, Bartolome and Gemmill 1981). Early human occupation of coastal California was accompanied by an increase in fire frequency (Knowles 1953) and a concomitant shift in the dominant vegetation (Aschmann 1959, Heusser 1978).

When the first Europeans entered California, grasslands were noted and it appears from diaries such as Fray Juan Crespi's that they were commonly in close proximity to Indian Villages and maintained through frequent Indian burning (Bolton 1927; Timbrook et al. 1982).

With European occupation came most of the annual grasses and forbs which now dominate the grasslands. These species were adapted to frequent disturbances such as fires and grazing through millenia of selection under such conditions in mediterranean Europe (Naveh 1967). Not only were these species resilient to disturbances, they were aggressive colonizers of such sites (Stebbins 1965). As land use intensified (Mooney and Dunn 1972) grasslands expanded. In the Los Angeles Basin during the second half of the 19th century, demand for grazing sites increased resulting in the conversion of brush covered sites to herbaceous vegetation (Burcham 1957). Historically, type conversion of this sort has been achieved by repeatedly burning coastal sage or chaparral (Sampson 1944; Arnold et al. 1951). These sites are readily colonized by grassland species and with successive fires their dominance increases. The process begins as a gradual thinning due to the fact that a portion of the resprouting shrub population, for all resprouting species, is killed in each successive fire and obligate seedling species require a decade or more to reach reproductive age (Keeley and Zedler 1978).

In the past 50 years land use practices have changed; in some areas grazing is less extensive and fire protection more effective. These changes have resulted in shrub reestablishment. Initially, coastal sage species are favored over chaparral

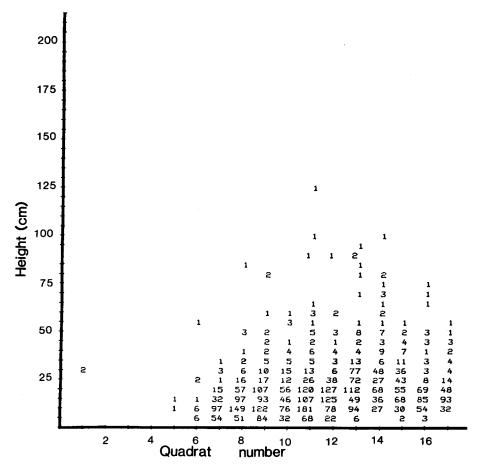


Fig. 4. Shrub height profile for Site 4 in the Calabasas Quadrangle.

species due to their higher dispersability (Wells 1962) and seeds which germinate readily without fire (Keeley and Keeley 1984). Such patterns of coastal sage invasion into grasslands following reduced disturbance were evident in several quadrangles (e.g., Thousand Oaks, Lake Mathews, and Laguna Beach) and similar patterns have been described by others (Haines 1966; McBride 1974; Westman 1976; Oberbauer 1978). The detailed studies of coastal sage demography patterns in the Calabasas Quadrangle (Fig. 3) suggest that a 10 year fire frequency, coupled with intensive grazing, are sufficient to inhibit sage invasion into grassland.

The hypothesis that disturbances such as grazing inhibit shrub invasion is at odds with the opinion of some (e.g., Dodge 1975 and others), who have suggested that grazing has enhanced coastal sage scrub invasion into grasslands in Southern California. Oberbauer (1978), however, points out that this opinion is based on extrapolation from other ecosystems such as desert grasslands where it has been demonstrated that grazing favors the spread of unpalatable spiny shrubs. Indeed, Oberbauer (1978) argues that one should not expect the same effect in coastal sage: grassland areas since the shrub species are not as noxious as thorny desert shrubs. Wells (1962) provided good evidence of the inhibitory effect of grazing

on coastal sage scrub and suggested that factors other than direct predation of seedlings could be involved, e.g., soil compaction and trampling. McBride and Heady (1968) also demonstrated that grazing inhibits the invasion of scrub vegetation into annual grasslands. Cessation of grazing and fires in their Berkeley Hills sites resulted in a return of scrub vegetation and a concomitant reduction in those grasslands. Similar conclusions were reached for Point Reyes Peninsula in northern California by Elliot and Wehausen (1974), for Santa Cruz Island by Brumbaugh (1980), and for the Santa Monica Mountains in southern California by Hobbs (1983).

Certain parts of the Los Angeles Basin, possibly due to increased population density, have experienced increased fire frequency. Here, grasslands have expanded at the expense of brush (particularly evident in Oat Mtn—Fig. 2, Calabasas, and Santa Susana quadrangles).

The patterns and processes involved in the vegetation mosaic in the Los Angeles Basin today are not unlike those in primeval times. The extent of grasslands has undoubtedly increased and the species composition has changed. The concept of a climax vegetation in this instance must be tempered with a recognition of the dynamic nature of the vegetations. Even so, successional patterns will be influenced to varying extents by species tolerances to such site characteristics as elevation, topography, aspect and substrate.

Literature Cited

- Arnold, K., L. T. Burcham, R. L. Fenner, and R. F. Grah. 1951. Use of fire in land clearing. Calif. Agric., 5(3):9-11, 5(4):145. 13. 15(5):11-12, 5(6):13-15, 5(7):6, 15.
- Aschmann, H. 1959. The evolution of a wild landscape and its persistence in southern California. Assoc. Amer. Geogr., Ann. 49 (Suppl. No. 3, Pt. 2):34-56.
- Bartolome, J. W., and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. Madrono, 28:172-184.
- Bolton, H. E. 1927. Fray Crespi-Missionary explorer on the Pacific Coast 1769-1774. Univ. Calif. Press, Berkeley. 402 pp.
- Brumbaugh, R. W. 1980. Recent geomorphic and vegetal dynamics on Santa Cruz Island, California. Pp. 139-158 in The California islands. Proceedings of a multidisciplinary symposium. (D. M. Power, ed.), Santa Barbara Mus. of Nat. Hist., Santa Barbara, Calif. 787 pp.
- Burcham, L. T. 1957. California range land; An historic ecological study of the range resources of California. State of Calif., Dept. of Nat. Res., Div. For. 261 pp.
- Clements, F. E. 1934. The relict method in dynamic ecology. J. Ecol., 22:39-68.
- Cooper, W. S. 1927. The broad-sclerophyll vegetation of California. Carnegie Inst. of Wash. Publ. No. 319. 124 pp.
- Cox, G. W. 1980. Laboratory manual of general ecology. William C. Brown Co., Dubuque, Iowa.
- Dodge, J. M. 1975. Vegetational changes associated with land use and fire history in San Diego County. Ph.D. Dissertation, Univ. Calif. Riverside. 216 pp.
- Elliot, H. W., III., and J. D. Wehausen. 1974. Vegetational succession on coastal rangeland of Point Reyes Peninsula. Madrono, 22:231-238.
- Fusch, R. D. 1968. Irvine Ranch: An analysis of changing land use patterns. M.S. Thesis, San Diego State Univ., San Diego, Calif. 120 pp.
- Goode, S. 1981. The vegetation of La Jolla Valley. M.S. Thesis, Calif. State Univ., Los Angeles. 45 pp.
- Haines, B. L. 1966. Invasion of grasslands and their inhibition by Artemisia californica Less. M.S. Thesis, Univ. Calif., Santa Barbara.
- Heady, H. F. 1977. Valley grasslands. Pp. 491-514 in Terrestrial vegetation of California. (M. G. Barbour and J. Major, eds.), Wiley-Interscience, New York.
- Heusser, L. 1978. Pollen in the Santa Barbara Basin, California: A 12,000-yr record. Geol. Soc. Amer. Bull., 89:673-678.

- Hobbs, E. R. 1983. Factors controlling the form and location of the boundary between coastal sage scrub and grassland in southern California. Ph.D. Dissertation, Univ. Calif., Los Angeles.
- Kay, B. L., R. M. Love, and R. D. Slayback. 1981. Discussion: Revegetation with native grasses. I. A disappointing history. Fremontia, 9(3):11-15.
- Keeley, J. E. 1981. Reproductive cycles and fire regimes. Pp. 231-277 in Proceedings of the conference fire regimes and ecosystem properties. (H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan and W. A. Reiners, eds.), USDA Forest Service, General Technical Report WO-26. 594 pp.
- . 1982. Distribution of lightning and man-caused wildfires in California. Pp. 431-437 in Proceedings of the symposium on dynamics and management of mediterranean type ecosystems. (C. E. Conrad and W. C. Oechel, eds.), USDA Forest Service, General Technical Report PSW-58. Berkeley. 637 pp.
- ——, and S. C. Keeley. 1984. Postfire recovery of California coastal sage scrub. Amer. Midl. Natur., 111:105-117.
- ——, and P. H. Zedler. 1978. Reproduction of chaparral shrubs after fire: A comparison of sprouting and seedling strategies. Amer. Midl. Natur., 99:142–161.
- Knowles, C. 1953. Vegetation burning by California Indians as shown by early records. Pamphlet 16, Fire Vol. 28, Forestry Library, Univ. Calif., Berkeley.
- Leak, W. B., and R. E. Graber. 1974. A method for deleting migration of forest vegetation. Ecology, 55:1425-1427.
- McBride, J. R. 1974. Plant succession in the Berkeley Hills, California. Madrono, 22:317-380.
- Mooney, H. A., and E. L. Dunn. 1972. Land-use history of California and Chile as related to the structure of the sclerophyll scrub vegetations. Madrono, 21:305-319.
- Naveh, F. 1967. Mediterranean ecosystems and vegetation types in California and Israel. Ecology, 48:445-459.
- Oberbauer, A. T. 1978. Distribution dynamics of San Diego County grasslands. M.S. Thesis, San Diego State Univ. Calif.
- Sampson, A. W. 1944. Plant succession on burned chaparral lands in northern California. Univ. Calif. Agric. Exper. Stn., Berkeley, Bull. No. 685. 144 pp.
- Stebbins, G. L. 1965. Colonizing species of the native California flora. Pp. 173-195 in The genetics of colonizing species. (H. G. Baker and G. L. Stebbins, eds.), Academic Press, New York.
- Stock, C. 1956. Rancho LaBrea—A record of Pleistocene life in California. Los Angeles Co. Mus. Nat. Hist., Sci. Ser. No. 20 Paleon No. 11 (6th ed).
- Timbrook, J., J. R. Johnson, and D. D. Earle. 1982. Vegetation burning by the Chumash. J. Calif. Great Basin Anthrop., 4:163-186.
- Wells, P. V. 1962. Vegetation in relation to ecological substratum and fire in the San Luis Obispo Quadrangle, California. Ecol. Monogr., 32:79-103.
- Wester, L. 1981. Composition of native grasslands in the San Joaquin Valley, California. Madrono, 28:231-241.
- Westman, W. E. 1976. Vegetation conversion for fire control in Los Angeles. Urban Ecol., 2:119-137.
- Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. Ecology, 64:809-818.
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